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Genetic Background and Environment Influence Palmitate Content of Soybean Seed Oil

G. J. Rebetzke,* V. R. Pantalone, J. W. Burton, T. E. Carter, Jr., and R. F. Wilson

ABSTRACT

Dietary concerns over high saturates contained in edible vegetable oils has stimulated development of soybean [*Glycine max* (L.) Merr.] cultivars with reduced palmitate content. Little is known of factors that might influence phenotypic expression of palmitate content among soybean populations varying for presence of a major reduced palmitate allele. The objective of this study was to investigate how environment and genetic background influence palmitate content when introducing the reduced palmitate trait into adapted backgrounds. Crosses were made between reduced palmitate germplasm, N87-2122-4 (53 g kg⁻¹ palmitate) and normal palmitate cultivars, A3733, Burlison, Kenwood, P9273, and P9341 (103–123 g kg⁻¹ palmitate). For each cross, F₄₆ lines homozygous for major reduced or normal palmitate alleles were bulked separately into Maturity Groups (MG) II, III, IV, and V, and evaluated in 10 contrasting field environments during 1993. Palmitate content varied between 82 and 90 g kg⁻¹ across southern U.S. and Puerto Rican environments. Much of this environmental variation was associated with changes in minimum temperature during the growing season. Genetic background effects were highly significant ($P < 0.01$) with cross means for palmitate content ranging between 81 and 93 g kg⁻¹. Across different maturity groups, palmitate content of the progeny was correlated ($r = 0.94$ – 0.99 , $P < 0.05$) with mean content of the normal palmitate parent, such that for every 1 g kg⁻¹ palmitate increase in the normal palmitate parent there was a 0.32 to 0.51 g kg⁻¹ palmitate increase in the progeny. Genetic background effects were presumed to be associated with action of minor alleles transmitted from the normal palmitate parent. Presence of the reduced palmitate allele was associated with significantly ($P < 0.01$) lower stearate (–6 to –13%) and higher oleate (+4 to +10%) contents across all maturity groups. Selection of low palmitate, high-yielding parents should further decrease palmitate content and produce correlated improvements in stearate and oleate contents to improve overall oil quality in progeny containing reduced palmitate alleles.

EPIDEMIOLOGICAL EVIDENCE and clinical studies alike have demonstrated that higher saturated fatty acid

intake contributes to raised blood serum cholesterol levels, thus increasing the risk of coronary heart disease (Willett, 1994; Uusitalo et al., 1996). Public perception of this potential health issue has provoked a strong trend towards greater consumption of foods containing lower levels of saturated fats (Wilson, 1991; Uusitalo et al., 1996). In turn, the U.S. Food and Drug Authority has proposed labeling regulations indicating “low saturate” vegetable oils must contain no greater than 70 g kg⁻¹ total saturates. Although soybean oil is relatively low in total saturates (≈ 120 – 200 g kg⁻¹), at least a minimum 50% reduction in saturated fat is needed to enhance the utility of soybean oil in this new market.

Palmitate is the predominant saturated fatty acid in soybean and most other vegetable oils (Weiss, 1983). Major alleles conditioning reduced palmitate content are available in soybean germplasm obtained from recurrent selection (Burton et al., 1994) and chemical mutagenesis (Horejsi et al., 1994; Wilcox et al., 1994). In response to consumer demand for healthful oils, soybean breeders are now actively incorporating the reduced palmitate trait into cultivar development programs (Burton et al., 1996). Given the need to transfer reduced palmitate alleles into a range of adapted, high-yielding genetic backgrounds (Wilson, 1991; Burton et al., 1996), it would be helpful to understand whether palmitate expression is contingent upon reduced palmitate genes contributed by the gene donor only, or genes present within both donor and adapted parents. The interaction of target genes with genes present within recipient genetic backgrounds can be an important consideration when introducing new traits into a commercial breeding program (Hallauer and Miranda, 1988). Further, it would be useful to document the influence of genetic background on expression of the reduced palmitate trait in different maturity zones and soybean production regions of the USA.

The influence of parental selection and genetic background on phenotypic expression for reduced palmitate content has not been reported for soybean. Earlier studies (Horejsi et al., 1994; Rebetzke et al., 1998) showed that palmitate content measured in different soybean

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populations reflected variation at both major and minor loci. The objective of this study was to evaluate the influence of environment and genetic background on palmitate content in soybean populations developed from crosses between reduced palmitate germplasm and normal palmitate cultivars.

MATERIALS AND METHODS

Reduced palmitate germplasm, N87-2122-4 (53 g kg⁻¹ palmitate), was used as a female in crosses to randomly selected midwestern cultivars, A3733, Burlison, Kenwood, P9273, and P9341 to generate five segregating populations. N87-2122-4 is of MG V and traces its pedigree to the reduced palmitate germplasm release, N79-2077-12 (Burton et al., 1994). The parental cultivars ranged in maturity from MG II to III and represented some of the highest-yielding midwestern cultivars at the time of the study. The F₁ plants were grown in Puerto Rico and harvested F₂ seed sown at Clayton, NC, in 1991. A 5-g seed sample was obtained from individually harvested F₂ plants and analyzed for fatty acid composition following Wilson et al. (1981). Seed containing either major alleles for reduced or normal palmitate can be genotyped from the quantity of palmitate found in their oil (Wilcox et al., 1994; Rebetzke et al., 1998). Eighty reduced and 80 normal palmitate progeny from each cross were selected and inbred through single-seed descent to the F_{4.5} generation. The reduced and normal palmitate classes were presumed to differ for presence or absence of the reduced palmitate allele described by Wilcox et al. (1994) and Rebetzke et al. (1998).

In 1992, a single row of each F_{4.5} line was grown at Clayton, NC, with MG I to VI check cultivars for the purpose of maturity designation. Seed was harvested and the putative reduced or normal palmitate genotype verified for each line by fatty acid analysis of seed oil following Rebetzke et al. (1998). Equal numbers of seed were then bulked for each cross from F_{4.6} lines of similar maturity (maximum maturity range in each bulk was 5 d) and either reduced or normal for palmitate content. Individual bulks were composites of between 12 and

15 lines. The inclusion of several random lines produced bulks that were putatively near-isogenic for maturity and major palmitate alleles but were random for minor palmitate alleles and alleles conditioning other traits.

The eight bulks per cross representing four maturity groups (MG I, II, IV, and V) and contrasting palmitate level were evaluated in 1993 along with parental (MG II–III) and non-parental (MG IV–V) check lines. Studies were conducted at three midwestern (Johnson City, IA; Napoleon, OH; St. Joseph, IL) and seven southern (Union City, TN; early and late sowing at Clayton, NC; Fletcher, NC; Plymouth, NC; Greenville, MS; Isabella, Puerto Rico) environments to provide a broad range of conditions during the growing season (Table 1). The MG II and III bulks were sown in the Midwest and at Union City, TN, while the MG IV and V bulks were sown in all seven southern environments. The experimental design at each location was a randomized complete block with three replicates. Three-row plots, 4.8 m in length and with 0.38 m between rows, were used at all locations except Fletcher (2.4-m-long plots); Greenville, Union City, and the Midwest (four-row plots, 6.1 m long). Seed was harvested at maturity from the center row(s) at each location. Maturity was determined for all plots as the date at which 95% of pods in the row obtained mature color. Seed from each plot was analyzed for oil composition following Rebetzke et al. (1998) and for seed oil content using near-infrared analyses by the USDA National Center for Agricultural Utilization Research (NCAUR), in Peoria, IL. Mean daily minimum and maximum temperatures were obtained for the growing season at all sites (Table 1).

A combined analysis of variance over environments was conducted on each maturity group for seed oil traits using the SAS procedure GLM (SAS Institute, 1990). Error variances for each environment were deemed homogenous following the Fmax test for homogeneity of error variances (Sokal and Rohlf, 1981). Palmitate content (reduced vs. normal bulks) was deemed a fixed effect, and crosses and environments random effects in deriving appropriate errors for statistical testing. Protected least significant differences (LSD) were calculated

Table 1. Environment means for seed oil quality characteristics measured in 1993 on soybean bulk populations representing soybean Maturity Groups (MG) II to V.

Environment	Fatty acid content					Oil content	Climate†		
	Palmitate	Stearate	Oleate	Linoleate	Linolenate		Rainfall	Temperature	
								Min.	Max.
	g kg ⁻¹					g kg ⁻¹	mm	°C	
Midwest USA (MG II)									
Mean	86	38	280	522	75	185	692	16.0	27.2
Min.	85	37	225	442	53	173	279	14.5	24.9
Max.	86	38	383	566	87	209	960	19.0	31.2
LSD‡	1	1	6	6	2	4			
Midwest USA (MG III)									
Mean	84	39	270	528	80	185	700	15.8	26.9
Min.	82	37	216	436	51	169	285	14.4	24.6
Max.	86	40	391	571	93	211	969	18.7	31.0
LSD‡	2	1	10	6	2	4			
Southeast USA (MG IV)									
Mean	86	38	358	462	56	207	298	19.3	30.8
Min.	82	36	330	396	46	183	168	16.1	28.3
Max.	90	42	436	506	66	224	396	21.9	32.1
LSD‡	2	1	14	14	2	4			
Southeast USA (MG V)									
Mean	88	38	344	474	57	204	307	18.9	30.9
Min.	82	35	309	418	47	186	171	15.0	27.7
Max.	89	42	410	505	66	223	403	21.9	31.9
LSD‡	2	1	12	10	2	4			

† Climate data based on period from sowing to harvest maturity.

‡ Approximate least significant difference ($P = 0.05$) for comparisons among environment means.

for comparisons among entries using the entry \times environment interaction mean square as the error from the expected mean squares.

RESULTS AND DISCUSSION

Time to maturity averaged over bulks in all populations was 113, 123, 119, and 126 d from sowing for MG II, III, IV, and V, respectively. Resulting differences in phenology combined with the breadth of environments over which studies were conducted produced a broad range of growing conditions from which response could be observed for all oil characteristics (Table 1). In turn, growing conditions appeared to have a large effect on all traits measured. Oil quality varied considerably between midwestern and southern growing regions, and among environments within each region. Seed oil content was generally greater for soybean bulks grown in the South (Table 1).

The Midwest and southern environments were characterized by similar palmitate and stearate contents (Table 1). This contrasted with Cherry et al. (1985), who reported large differences for saturated acid content between northern and southern soybean regions. However, such contrasts were confounded with cultivar differences, while bulks in this study represented the same average genetic background, differing only for loci controlling maturity. Variability for palmitate content among locations within the South was greater than for the Midwest (Table 1). Palmitate content ranged between 82 and 90 g kg⁻¹ among southern environments compared with 82 to 86 g kg⁻¹ in the Midwest. Oleate content was about 25% greater in the South than in the Midwest, while reduced oleate in the Midwest was compensated for by increased desaturation to linoleate and linolenate. In turn, linolenate content was greater in the Midwest than in the South.

Variation in oil composition appeared to reflect differences in temperatures prevailing at each environment. The higher proportion of oleate in oil collected from warmer southern environments was consistent with high oleate in soybean seed developing under warmer temperatures in controlled environment (Rennie and Tanner, 1989) and sowing date (Kane et al., 1997) studies. High oleate content follows from inhibition of the oleoyl desaturase system at high air temperatures (Cheesbrough, 1989). Equally, high linolenate content at cooler temperatures follows from other studies (e.g., Wilcox and Cavins, 1992; Kane et al., 1997) and presumably reflects enhanced activity of the lineoyl desaturase system at cooler air temperatures (Cheesbrough, 1989).

Although regional effects exerted minor influence upon palmitate content, certain distinction was noted for location effects particularly in the South (Fig. 1). Palmitate content in MG IV and V bulks could be used to separate southern environments into three groups based on mean daily minimum temperature at each location: Fletcher, NC (15.5°C), Puerto Rico (21.9°C), and all other environments (19.1°C). When all southeastern environments were considered, mean daily minimum temperature explained 87 to 94% ($P < 0.01$) of the MG IV and V among-environment palmitate variance

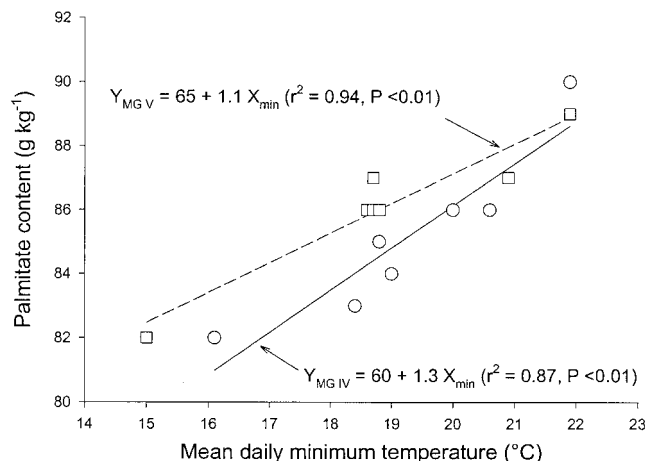


Fig. 1. Relationship between palmitate content and mean daily minimum temperature for Maturity Group IV (○) and V (□) soybean bulks grown in the southeastern USA and Puerto Rico in 1993.

(Fig. 1). This apparent temperature response was similar to findings of Rennie and Tanner (1989), who reported a large increase in palmitate content of soybean grown from 15/12°C (day/night) to 40/30°C. Similarly, Wilcox and Cavins (1992) reported reductions in palmitate content for soybean maturing into increasingly cooler air temperatures.

There was substantial phenotypic variation for palmitate content measured in all maturity groups (Table 2). More than 95% of this variation was attributable to differences in palmitate content among tested entries. Furthermore, among-entry differences were considerably greater than differences associated with the interaction of entries with environments. The relative sizes of entry to interaction mean squares were consistent across maturity groups representing very different production regions within and outside the USA. The lower entry \times environment interaction suggests that selection within maturity groups for average response across environments should produce soybean lines with desired palmitate levels. The relatively small entry \times environment interaction for palmitate content was consistent with previous studies for lines and cultivars grown in multiple environments (Hawkins et al., 1983; Horejsi et al., 1994; Rebetzke et al., 1996).

Much of the among-entry variation was associated with differences among progeny, particularly between reduced and normal palmitate bulks (Table 2). The latter represents differences among alleles associated with segregation at a single major reduced palmitate locus. Reduced palmitate bulks produced an average 40% less palmitate than normal bulks evaluated in all maturity groups (Tables 3 and 4). Differences in the effect of the reduced palmitate allele were consistent in size with differences observed among F_{5:7} soybean inbreds varying for reduced and normal palmitate content (Rebetzke et al., 1998). Progeny bulks grown in the MG II and III studies produced significantly ($P < 0.01$) less palmitate than their midwestern parents (Table 3). For example, P9273 and P9341 produced about 30% greater palmitate content than the mean of their reduced and normal

Table 2. Analysis of variance for palmitate content measured on Maturity Groups (MG) II, III, IV, and V reduced and normal palmitate bulk soybean populations.

Source	MG II		MG III		MG IV		MG V	
	df	MS	df	MS	df	MS	df	MS
Environments	3	5	3	104**	6	161***	6	117***
Reps (Environments)	8	4**	8	7**	14	7	14	13*
Entries	12	6 149***	14	6 364***	10	10 951***	10	10 532***
Parent(s) vs. progeny bulks†	4	684***	4	738***	1	7 820***	1	8 823***
Among normal parents (MG II & III only)	1	26 742***	1	31 506***	—	—	—	—
Among progeny bulks	7	6 330***	9	6 071***	9	11 299***	9	10 721***
Reduced vs. normal palmitate bulks	1	43 057***	1	53 704***	1	99 430***	1	92 972***
Among reduced palmitate bulks	3	99***	4	49***	4	31**	4	204***
Among normal palmitate bulks	3	318***	4	184***	4	534***	4	677***
Entry × environment (E)	36	8***	42	8***	60	10***	60	18***
Among normal parents × E	12	13***	12	7***	—	—	—	—
Parents vs. progeny bulks × E	3	17*	3	30***	6	28***	6	30***
Among progeny bulks × E	21	3*	27	6***	54	9***	54	17***
Reduced vs. normal palmitate bulks × E	3	3	3	6***	6	27***	6	42***
Among reduced palmitate bulks × E	9	2	12	4*	24	5	24	10*
Among normal palmitate bulks × E	9	4*	12	8***	24	7**	24	17***
Pooled error	96	2	112	2	140	4	140	6

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level.

† Parents were adapted cultivars for MG II and III, and N87-2122-4 for MG IV and V.

progeny. There were also large differences for palmitate content among progeny bulks homozygous for reduced or normal major palmitate alleles (Table 2). For example, MG V reduced and normal palmitate bulks ranged between 61 and 70 and between 102 and 116 g kg⁻¹ palmitate, respectively (Table 4). The sizes of such differences were repeatable for reduced and normal palmitate bulks grown in all maturity groups (Tables 3 and 4) and appear to reflect variation arising through minor gene differences.

Phenotypic variation was also attributed to significant ($P < 0.01$) differences in mean palmitate content among crosses (Table 2). Cross means ranged between 81 and 93 g kg⁻¹ palmitate (Fig. 2). Because a single reduced palmitate donor was used to generate all populations tested, all of the differences between cross means must have arisen through genetic differences among normal

palmitate parents. This is supported by evidence gained from observations on both parents and progeny. First, large significant ($P < 0.01$) differences were observed among normal palmitate parents in the MG II and III studies (Table 2). Mean palmitate contents averaged over four midwestern locations were 109, 103, 123, 108, and 116 g kg⁻¹ for parental cultivars A3733, Burlison, Kenwood, P9273, and P9341, respectively. Kenwood produced about 20% greater palmitate content than Burlison, but only 6% higher palmitate than P9341. Second, palmitate content varied among reduced and normal palmitate bulks homozygous at the major reduced palmitate locus. Relationships between palmitate content of each normal palmitate parent and mean palmitate content of its progeny were strong ($r = 0.94$ – 0.99 , $P < 0.05$) and repeatable across bulks representing the broad range of maturity groups and environments sampled

Table 3. Seed composition for checks and Maturity Group (MG) II and III reduced and normal palmitate soybean bulks grown in the midwestern USA during 1993.

Entry	Palmitate class	Fatty acid content								Oil content		Protein content	
		Palmitate		Stearate		Oleate		Linolenate					
		MG II	MG III	MG II	MG III	MG II	MG III	MG II	MG III	MG II	MG III	MG II	MG III
		g kg ⁻¹											
Palmitate bulks													
N87-2122-4 × A3733‡	Reduced	–	61	–	39	–	260	–	83	–	186	–	413
N87-2122-4 × A3733‡	Normal	–	107	–	44	–	263	–	77	–	193	–	401
N87-2122-4 × Burlison	Reduced	62	62	32	32	292	304	74	75	186	183	424	420
N87-2122-4 × Burlison	Normal	103	100	35	38	277	260	73	74	179	182	430	425
N87-2122-4 × Kenwood	Reduced	68	66	37	37	257	259	84	86	179	181	412	405
N87-2122-4 × Kenwood	Normal	113	109	41	39	268	258	68	75	187	187	414	408
N87-2122-4 × P9273	Reduced	63	63	35	35	287	282	76	81	188	185	417	411
N87-2122-4 × P9273	Normal	102	102	40	41	265	253	74	76	189	188	409	407
N87-2122-4 × P9341	Reduced	66	62	40	35	306	304	75	83	188	186	410	405
N87-2122-4 × P9341	Normal	110	107	41	40	284	262	73	83	184	184	410	406
LSD (0.05)		1	2	2	2	17	22	4	5	5	7	12	15
Checks‡		108	116	37	37	239	244	74	80	210	198	391	398
LSD (0.05)§		2	2	1	2	32	35	5	7	6	8	14	15

† Progeny were unavailable from A3733 in the MG II study.

‡ Check cultivars were P9273 and P9341 for MG II and MG III studies, respectively.

§ Least significant difference for comparisons among bulk and check means.

Table 4. Seed composition for checks and Maturity Group (MG) IV and V reduced and normal palmitate soybean bulks grown in the southern USA and Puerto Rico during 1993.

Entry	Palmitate class	Fatty acid content										Oil content		Protein content	
		Palmitate		Stearate		Oleate		Linolenate							
		MG IV	MG V	MG IV	MG V	MG IV	MG V	MG IV	MG V	MG IV	MG V	MG IV	MG V		
		g kg ⁻¹													
Palmitate bulks															
N87-2122-4 × A3733	Reduced	62	66	42	41	372	380	57	55	214	214	426	431		
N87-2122-4 × A3733	Normal	105	105	44	43	357	351	54	54	212	209	419	424		
N87-2122-4 × Burlison	Reduced	63	61	33	33	362	350	58	60	198	198	430	440		
N87-2122-4 × Burlison	Normal	102	104	37	36	333	310	57	59	194	196	431	447		
N87-2122-4 × Kenwood	Reduced	65	70	39	39	359	306	58	62	208	203	417	422		
N87-2122-4 × Kenwood	Normal	113	116	43	44	325	289	55	60	204	205	413	423		
N87-2122-4 × P9273	Reduced	64	64	36	37	374	383	56	53	215	211	429	424		
N87-2122-4 × P9273	Normal	103	102	39	39	336	353	55	53	211	204	429	424		
N87-2122-4 × P9341	Reduced	62	64	36	38	407	372	57	59	209	206	426	430		
N87-2122-4 × P9341	Normal	111	110	39	38	351	347	59	59	204	199	424	425		
LSD (0.05)		2	3	1	2	16	19	2	2	3	8	13	14		
Checks†		116	120	39	36	245	201	68	81	216	204	413	410		
LSD (0.05)‡		2	3	1	2	17	19	2	3	3	4	13	13		

† Check cultivars were P9442 and Essex for MG IV and MG V studies, respectively.

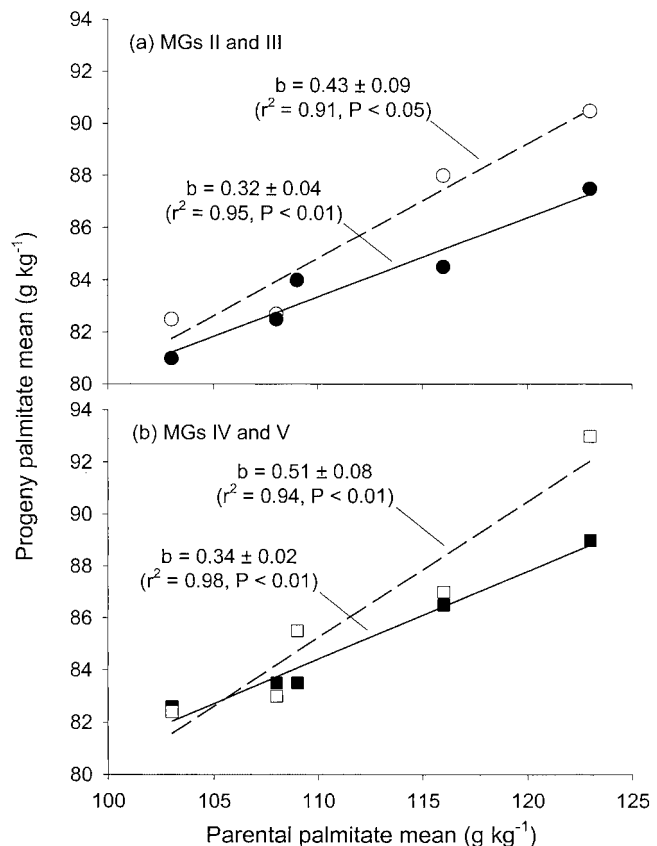
‡ Least significant difference for comparisons among bulk and check means.

(Fig. 2). Furthermore, these relationships were linear such that there was a 0.32 to 0.51 g kg⁻¹ palmitate increase in the progeny for every 1 g kg⁻¹ palmitate increase in the normal palmitate parent. This suggests that development of soybean populations from normal palmitate parents producing 30 g kg⁻¹ lower palmitate content can reduce mean palmitate content in the progeny by up to 16 g kg⁻¹, or 1.6% of total oil.

Rebetzke et al. (1998) demonstrated that reduced palmitate content in soybean oil was conditioned by both major and minor alleles. Effects associated with modifying gene action were small but heritable in homozygous reduced and normal inbred lines for a range of crosses representing different genetic backgrounds. The linear relationship observed between parent and progeny in this study corroborated earlier evidence that phenotypic differences among parents reflect variation for the presence of minor genes. Furthermore, the strong nature of this linear relationship suggests that genetic effects are accumulated in an additive manner.

An understanding of the influence of palmitate content on seed oil quality is necessary for breeders wishing to introduce the reduced palmitate trait into soybean cultivars. Observations on associated traits were made simple in this study through use of near-isogenic bulk populations contrasting for a single major reduced palmitate allele. Significant ($P < 0.01$) reductions in palmitate content produced concomitant changes in oil quality (Tables 3 and 4). Oil content remained unchanged for reduced and normal palmitate bulks grown in the Midwest, while oil content was greater for reduced palmitate bulks grown in the South. Selection for reduced palmitate content produced no change in seed protein content (Tables 3 and 4) or seed quality appearance (data not shown). Stearate, the other major saturated fatty acid in soybean oil, was significantly ($P < 0.05$) lower, and the monounsaturated oleate significantly ($P < 0.05$) higher, for reduced palmitate bulks grown in both the Midwest and South (Tables 3 and 4). Fur-

thermore, oleate was significantly ($P < 0.01$) greater for all bulks than commercial checks evaluated in mid-western and southern environments. Resulting changes in stearate and oleate contents through selection for reduced palmitate content should enhance the overall nutritional quality of soybean oil (Grundy, 1986). Dif-

**Fig. 2.** Relationship between palmitate content of the normal palmitate soybean parent and the bulk mean of its reduced and normal palmitate progeny for Maturity Groups: (a) II (○) and III (●); and (b) IV (■) and V (□).

ferences in linolenate content between reduced and normal palmitate bulks were contingent on the maturity group in which bulks were evaluated. Quantity of palmitate had little or no effect on linolenate content of bulks grown in the South, while reduced palmitate bulks grown in the Midwest were generally higher in linolenate content. However, the small nature of this increase (75 vs. 80 g kg⁻¹ oil averaged over bulks) is unlikely to have any greater effect on oil stability than for oil collected from normal bulks (Wilson, 1991).

In conclusion, any factor that increases palmitate content will increase total saturates. This study has shown that environment and genetic background have the potential to increase palmitate content above the 70 g kg⁻¹ saturate threshold necessary for reduced saturate vegetable oils. Warmer temperatures will increase the level of palmitate in the processed oil, the extent being somewhat predictable based on regional temperatures up to physiological maturity. Breeders must also consider the effect of the high-yielding parent when making crosses aimed at the development of high-yielding, reduced palmitate cultivars. Higher palmitate cultivars will produce higher palmitate progeny owing to minor genes contributing to variation for palmitate content. Selection of lower palmitate, high-yielding parents when incorporating reduced palmitate alleles will produce populations with decreased palmitate content. Correlated improvements in stearate and oleate contents together with reduced palmitate should improve overall oil quality.

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